EXPERIMENTAL STUDIES ON NATURAL SELECTION FOR TIME OF HEADING AND ITS INNER FACTORS IN SOME BARLEY HYBRID POPULATIONS

II. Genotypic Constitutions of Selection Lines Derived from the Populations Grown at Different Locations

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I. INTRODUCTION

In the previous study with some barley hybrid populations which had been grown in bulk during several successive generations at different locations, it was confirmed that natural selection had a remarkable influence upon heading time and its inner factors, namely, spring and winter habit of growth and sensitivities to photoperiod after vernalization (Yasuda, 1961).

Afterwards, the early, mid-season and late type plants were selected among F_6 populations at each of the different locations, and their genotypic constitutions for heading time and its inner factors were investigated. The results obtained will be presented below.

II. MATERIALS AND METHODS

The cross combinations and the characteristics of their parental varieties are as shown in Table 1. These two hybrid populations were each grown in

TABLE 1
Cross combinations and characteristics of their parental varieties

Cross No.	Parent	Origin	Earliness (Fall-sown)	Grade of spring habit	Growth habit genes involved*	Sheath hair
1	Iwate Omugi No. 1	Iwate	very late	VI	$ShSh\ sh_2sh_2$	hairy
	Indian Barley	Formosa	very early	I	$ShSh\ Sh_2^ISh_2^I$	hairy
3	Kuromugi No. 148	Shizuoka	early	II	$ShSh\ Sh_2^{II}Sh_2^{II}$	hairy
	Mensury C	Iwate	very late	I	$shsh\ sh_2sh_2$	none

* sh and Sh_2 are genes for spring habit.

bulk from F_2 up to F_5 generation in successive years since the fall of 1954 at the four locations; namely, Morioka, Konosu, Kurashiki and Kanoya which are located in northern, central, southern and southernmost of Japan, respectively. Hybrid populations, each consisted of about 2400 plants, were cultivated after the conventional growing method of the respective places.

In the fall of 1958, about 300 seeds per cross were randomly taken from the F_5 hybrid seeds, and space planted at each location. Thirty earliest plants and 15 latest plants were selected from each of the populations of both crosses. They will be called as early and late selections, respectively. About 15 mid-season selections were also taken from each population, which headed just about the time of modal date of the populations. These selections were used as the materials for analysis at Kurashiki. The characters and methods of analyses are as follows:

(1) Time of heading in open field: The seeds of each selection together with those of their parental varieties were simultaneously sown in the field with two replications in November 15 at Kurashiki. Number of plants used are 40 plants per line. Manuring and other cultivating practice were made according to the conventional methods. Records were taken for heading date of the earliest plant within line and also for the date when about 80 percent of plants of each line had appeared. The time of heading of each of the lines has been shown as an average of these two values, because the average value may represent the line mean of heading date recorded on single plant basis.

(2) Genotypic constitution for spring and winter habit of growth: About 30 plants in each of lines from different locations were reared throughout under 24 hour day in a greenhouse. The natural day-light were supplemented by incandescent lamps. Days to flag-leaf emergence and number of leaves on the main stem were recorded. The character for hairy and non-hairy sheath was also investigated for Cross No. 3.

(3) Response to short-day (photoperiodic response): Slightly sprouted seeds of each line and those of the parental varieties were fully vernalized prior to planting by exposing to low-temperature of 1～3°C for 60 days, and grown in a greenhouse under 8 hour day for 40 days and thereafter under 24 hour day. Number of plants tested are 20 plants per line. Daily records of each of the plants were taken for date of flag-leaf emergence and number of leaves on the main stem.

(4) Response to long-day (earliness in a narrow sense): An investigation was run only in the lines derived from Morioka and Kurashiki populations. After vernalization, 20 germinated seeds per line and those of parental varieties were sown in wooden flats and reared throughout under 24 hour day in a greenhouse. The date of flag-leaf emergence and number of leaves on the main stem were recorded on the single plant basis. You can find the details of these analytical methods in the previous report (Yasuda, 1961).

III. EXPERIMENTAL RESULTS

1. *Time of Heading in the Open Field*

Group means and variances within group for heading time under outdoor conditions are shown in Table 2.

TABLE 2

Group means and variances within group in heading time of selection line groups from four locations when they were simultaneously sown outdoors in fall at Kurashiki

(A) Cross No. 1 : Iwate Omugi No. 1 × Indian Barley

Location	Early group		Mid-season group		Late group	
	Mean*	Variance	Mean*	Variance	Mean*	Variance
Morioka	16.04	5.1233	27.80	29.6357	43.90	7.8643
Konosu	25.29	25.7660	31.36	0.6413	35.13	5.1667
Kurashiki	15.46	30.5874	30.72	3.8760	40.77	21.2452
Kanoya	19.68	23.7477	26.91	19.8909	29.00	6.2143

Parent (mean) : Iwate Omugi No. 1 43.00 ; Indian Barley 13.56

* Number of days from April 1st.

(B) Cross No. 3 : Kuromugi No. 148 × Mensury C

Location	Early group		Mid-season group		Late group	
	Mean*	Variance	Mean*	Variance	Mean*	Variance
Morioka	26.89	3.4138	30.23	3.2988	36.29	10.1117
Konosu	22.18	6.7088	28.42	5.6288	32.33	5.5606
Kurashiki	25.05	6.5233	27.75	6.2500	36.17	13.1970
Kanoya	25.65	7.2784	27.54	1.6117	32.03	8.1984

Parent (mean) : Kuromugi No. 148 21.75 ; Mensury C 34.75

* Number of days from April 1st.

Table 2 shows that the group mean of heading time is always the smallest in the early selection groups which are followed by the mid-season and finally by the late selection groups. Their differences prove to be significant. This naturally means that the selections derived as an early type at respective locations always head earlier than those of the other types, when they have simultaneously been sown outdoors in fall at Kurashiki.

A glance at Table 2 reveals that average heading time of the selection group tends to become earlier, though slightly, as their growing locations go down to south. This is almost as expected from the analysis of their original populations (Yasuda, 1961). However, Table 2 differed slightly from the expectation from the results in the populations : The heading time of the early selection group in Cross No. 1 is markedly earlier in those from Morioka (north), and is not necessarily earlier in those from Kanoya (southernmost). Furthermore, retardation of heading time in the late selection group from Kurashiki (south) is evident in both crosses as well as those from Morioka.

These results, however, does not give the clearcut explanation about the problem how many and to what extent early or late lines are involved in each group of the selections. In order to make these points clear, frequency distributions of the lines in each of the selection groups from different locations are compared, which are shown in Figs. 1 and 2.

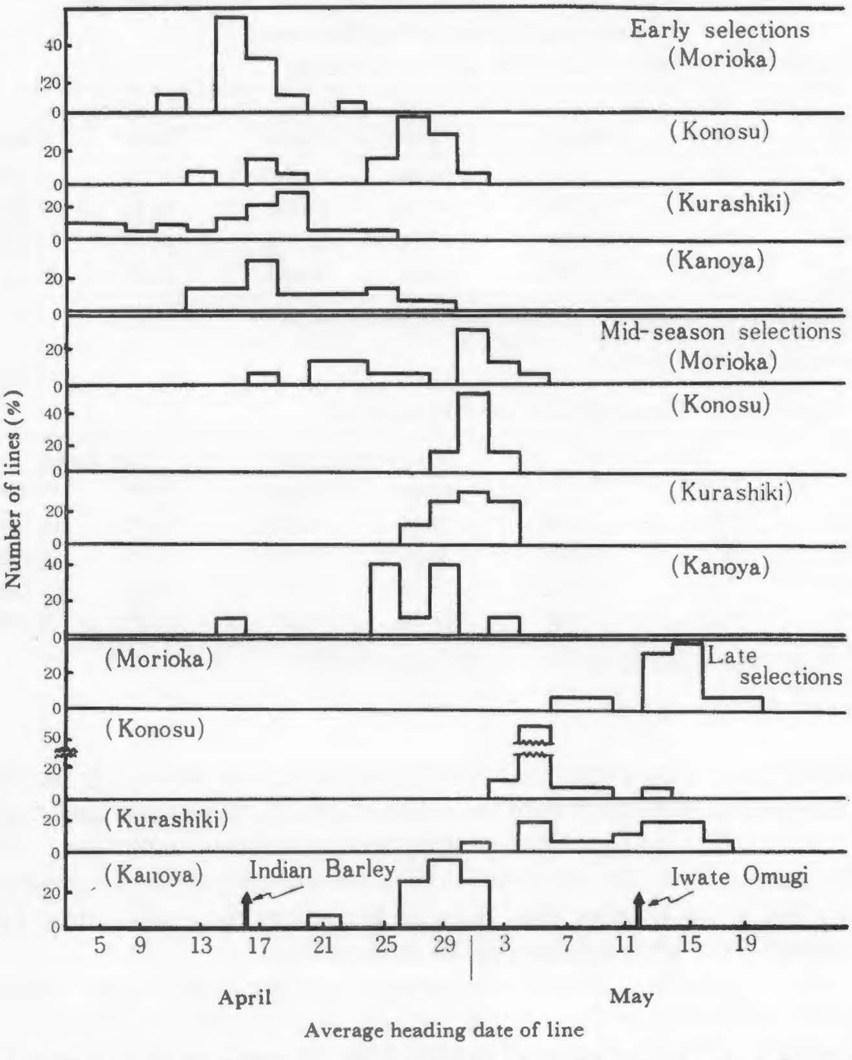

Fig. 1. Frequency distribution regarding the heading date of the selections from four locations and their parents in Cross No. 1. Seeds were sown outdoors in November 15 at Kurashiki.

First, the results of the early selection groups from the two crosses will be stated. As seen in Fig. 1, the largest number of extremely early lines are involved in Kurashiki selections: About one third of them was earlier than the very early parent, Indian Barley, and a line exceeded 10 or more days. However, almost all of the early selection lines from the other three locations

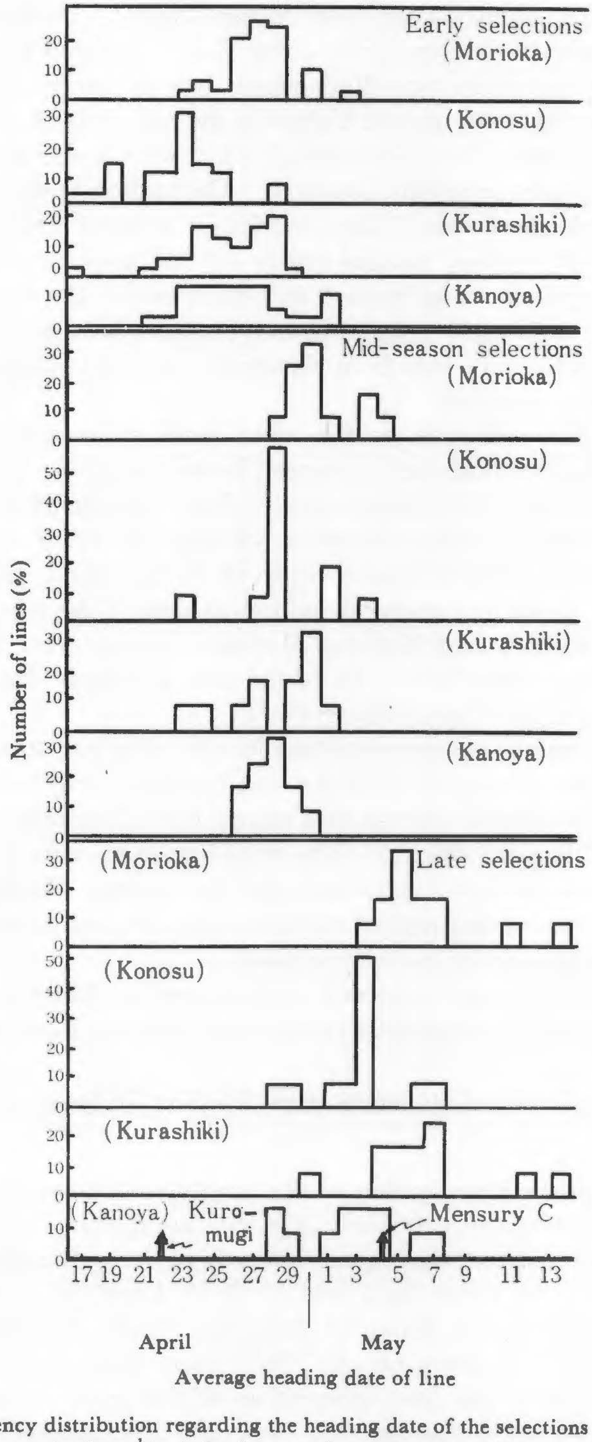

Fig. 2. Frequency distribution regarding the heading date of the selections from four locations and their parents in Cross No. 3. Seeds were sown outdoors in November 15 at Kurashiki.

were similar to or slightly later than Indian Barley. In Cross No. 3, the situation is somewhat different from Cross No. 1. As shown in Fig. 2, the proportion of transgressive type lines which headed earlier than the early parent, Kuromugi No. 148, was the highest in the early selections from Konosu (35%), followed by those from Kurashiki (7%). Not a single line as such was found among Morioka selections, however. The earliest lines in both Konosu and Kurashiki selections were 5 days earlier in average heading time than Kuromugi No. 148. Thus, location-effects on the appearance of the early transgressive type lines are so marked in both crosses. However, it must be noted, here, that such early transgressive type lines have never been found among the early selection group from Kanoya in spite that Kanoya is lowest in latitude among four locations.

Among the late selections, on the other hand, transgressive lines which head rather much later than the late parent, Iwate Omugi No. 1 in Cross No. 1 or Mensury C in Cross No. 3, may deserve of our consideration. They were found most abundantly among Morioka selections of Cross No. 1. Though much less in number, they were also involved in Kurashiki selections of the same cross. The latest line among them headed about 6 days later than Iwate Omugi No. 1. Konosu and Kanoya selections, on the other hand, did not involve such transgressive lines. All of the late lines from Kanoya were 10 days or more earlier than Iwate Omugi No. 1.

A similar situation was seen in Cross No. 3. The late transgressive lines were very frequent among the Morioka and Kurashiki selections, while there were only two transgressive lines as such among each of the late selection groups from Konosu and Kanoya (Fig. 2). The latest line from each of Morioka and Kurashiki populations was 9 days later the late parent, Mensury C. These results clearly indicated that natural selection had operated strongly on the late type plants, as well as on the early type plants.

There were no definite tendency with regard to differences in time of heading among mid-season selection groups from different locations.

2. *Comparison of Genotypic Constitutions of the Selections for Spring and Winter Habit of Growth*

The results of the investigation on the genotypic constitution of the selections for their spring and winter habit of growth are illustrated in Tables 3 and 4. It will be expected that the segregation ratio of the spring and winter types in F_2 hybrid is 3 : 1 for Cross No. 1 and 13 : 3 for Cross No. 3, because Cross No. 1 has involved only one dominant gene pair $Sh_2^I Sh_2^I$ and Cross No. 3 one recessive (*shsh*) and one dominant ($Sh_2^{II} Sh_2^{II}$) gene pairs for spring habit of growth (Table 1). In the later generation of the latter cross (No. 3), five different genotypes can be distinguished from each other among the spring type plants. The reasons are as follows : The genes *Shsh* are linked with the genes

Hshs for sheath hair with 6–7% of recombination, and a plant with the gene pair *shsh* (grade I for spring habit) is definitely earlier in heading under continuous illumination at high temperature than that with only gene pair $Sh_2^{II}Sh_2^{II}$ (grade II) (Takahashi *et al.* 1951, 1954, 1956). Consequently, the visual differences in hairy condition on leaf sheath and in heading times under continuous illumination made it possible to distinguish a plant with genotype of $shshSh_2^{II}Sh_2^{II}$, $shshSh_2^{II}sh_2$ or $shshsh_2sh_2$ (these three types can not be discriminated because of the epistasis of *shsh* over $Sh_2^{II}Sh_2^{II}$) from the one with genotype $ShShSh_2^{II}Sh_2^{II}$ ($- -\ Sh_2^{II}sh_2$) or $ShshSh_2^{II}Sh_2^{II}$ ($- -\ Sh_2^{II}sh_2$).

It is apparent from the Tables 3 and 4 that winter type lines predominate

TABLE 3
Genotypic constitutions for spring and winter habit of growth in selection lines of Cross No. 1 (Iwate Omugi No. 1×Indian Barley) from four locations

Selection group	Location	Spring type		Winter type	Total
		$Sh_3^I Sh_3^I$	$Sh_3^I sh_3$	sh_3sh_3	
Early	Morioka			24	24
	Konosu	18	1	3	22
	Kurashiki	16	2	9	27
	Kanoya	25			25
Mid-season	Morioka		1	14	15
	Konosu	13		5	18
	Kurashiki	12		3	15
	Kanoya	9	1	1	11
Late	Morioka		1	14	15
	Konosu	11	1	3	15
	Kurashiki	5	1	9	15
	Kanoya	12		3	15
Total (%)	Morioka	0(0)	2(3.7)	52(96.3)	54(100)
	Konosu	42(76.4)	2(3.6)	11(20.0)	55(100)
	Kurashiki	33(57.9)	3(5.3)	21(36.8)	57(100)
	Kanoya	46(90.2)	1(2.0)	4(7.8)	51(100)
	Theoretical	(48.3)	(3.4)	(48.3)	(100)

in Morioka selections and also are mostly homozygous for winter genes. On the other hand, the selections from the locations south to Konosu included consist chiefly of spring type lines which almost all of them are homozygous for spring genes, though the number and kinds of spring genes involved in the crosses are not the same. It is noted that in the early selections of Cross No. 1, spring type lines are not found in Morioka selections, while winter type ones are lacked in Kanoya selections. However, it must be mentioned that the frequencies of spring or winter type lines in the late selections differed slightly with the

TABLE 4
Genotypic constitutions for spring and winter habit of growth in selection lines of Cross No. 3 (Kuromugi No. 148×Mensury C) from four locations

Selection group	Location	Spring type					Winter type		Total
		Homozygous			Heterozygous		Hetero.	Homo.	
		aabb* aaBB aaBb	AaBB	AABB	AaBb	AABb	Aabb	AAbb	
Early	Morioka	1		2	1	2	1	22	29
	Konosu	12	2	15			1		30
	Kurashiki	16		10	1	1		2	30
	Kanoya	15		13		1		1	30
Mid-season	Morioka	1	1		2		1	7	12
	Konosu	8		3				1	12
	Kurashiki	6		5				1	12
	Kanoya	6	1	3				2	12
Late	Morioka	3	1	1				7	12
	Konosu	6		1		1		4	12
	Kurashiki	5	1	1			1	4	12
	Kauoya	5		2	1	1	1	2	12
Total (%)	Morioka	5(9.4)	2(3.8)	3(5.7)	3(5.7)	2(3.8)	2(3.8)	36(67.9)	53(100.1)
	Konosu	26(48.1)	2(3.7)	19(35.2)		1(1.9)	1(1.9)	5(9.3)	54(100.1)
	Kurashiki	27(50.0)	1(1.9)	16(29.6)	1(1.9)	1(1.9)	1(1.9)	7(13.0)	54(100.1)
	Kanoya	26(48.1)	1(1.9)	18(33.3)	1(1.9)	2(3.7)	1(1.9)	5 (9.3)	54(100.1)
	Theoretical	(47.7)	(0.8)	(23.5)	(3.0)	(0.8)	(0.8)	(23.5)	(100.1)

* Aa and Bb stand for the gene pairs *Shsh* and $Sh_2^{II}sh_2$, respectively.

crosses. Namely, in Morioka selections, proportion of spring type lines within group is markedly higher in Cross No. 3 than in Cross No. 1. Furthermore, in Kurashiki selections, the frequency of winter type line is much higher in Cross No. 1 than in Cross No. 3. But, whether or not such differences in frequency of spring or winter type lines between crosses are caused by the difference in genes for growth habit is difficult to interpret with certainty, because it may be possible that number of lines tested is too small to draw a decisive conclusion.

Tables 3 and 4, furthermore, show that the frequencies of winter type line in the selections from Konosu and other southern locations tend to become higher slightly in the order of the early, mid-season and late selection groups. Such a tendency is more pronounced in Cross No. 3. On the contrary, in Morioka selections, no differences in frequencies of spring and winter type lines are found among three selection groups in each of crosses.

As has already been stated, two kinds of spring genes, *sh* and Sh_2^{II}, are involved in Cross No. 3, so that the homozygous lines for spring genes can be further divided into three types by the difference of their genotypic constitutions

(Table 4). It will be seen from the table that the frequencies of spring type lines are different with their genotypic constitutions even in the selections from the same location. In the selections from the locations south to Konosu included, the $ShShSh_2{}^{II}Sh_2{}^{II}$ type lines are about 10 percent higher in frequency than the expected, while the frequencies of the other spring genotypes are almost the same as the expected. It seems, therefore, that the increase in $ShShSh_2{}^{II}Sh_2{}^{II}$ type has resulted in the predominance of spring types on the low latitudinal locations.

3. *Responses of Vernalized Plants to Short-day (Photoperiodic Response)*

Tables 5A (Cross No. 1) and 5B (Cross No. 3) give the group means and variances within group for number of days to flag-leaf emergence under short-day condition at high temperature after vernalization.

TABLE 5

Group means and variances within group in days to flag-leaf emergence under short-day at high temperature after vernalization

(A) Cross No. 1 : Iwate Omugi No. 1×Indian Barley

Location	Early group		Mid-season group		Late group	
	Mean	Variance	Mean	Variance	Mean	Variance
Morioka	64.12	11.5350	66.80	28.8457	75.89	9.4691
Konosu	63.16	3.6777	64.03	1.6963	66.14	3.3769
Kurashiki	60.68	30.7503	64.44	3.9326	71.64	17.5926
Kanoya	61.70	1.8375	63.33	5.8642	66.23	7.2352

Parent : Iwate Omugi No. 1 77.72, 1.4964 : Indian Barley 59.55, 0.7428

(B) Cross No. 3 : Kuromugi No. 148×Mensury C

Location	Early group		Mid-season group		Late group	
	Mean	Variance	Mean	Variance	Mean	Variance
Morioka	82.32	16.3393	85.03	48.9090	87.61	21.8677
Konosu	77.63	16.2913	80.34	17.0938	87.58	25.4773
Kurashiki	77.89	15.9186	82.16	13.5060	87.62	15.6840
Kanoya	77.06	7.2988	78.69	16.3236	85.58	12.0107

Parent : Kuromugi No. 148 77.20, 2.0091 : Mensury C 93.80, 1.9187

It can be seen in Table 5 that group mean is always the smallest in the early selection groups which are followed by the mid-season and finally by the late selection groups, their differences being between 2 and 7 days. It is also apparent in the same table that the selection groups from Kanoya are always earliest, and that those from Morioka are later than others. This situation is especially conspicuous in Cross No. 1. These imply that plants insensitive to short-photoperiod or day-neutral type plants which head earlier under short-day at high temperature after vernalization are abundantly included in Kanoya selections, but a few or none of such type plants are found in Morioka selections. The group means of the Konosu and Kurashiki selections are not so much different in most cases, however.

The variances within group are larger in the selection groups from Morioka and smaller in those from Kanoya, though there are some exceptions in Cross No. 1.

It must be admitted, however, that such results give only outlines of responses of different selection lines to short-day. When these different selection lines were simultaneously grown in fall at Kurashiki, variations in heading time within group were found in each of their groups, and the proportions of very early or very late type lines included in their groups differed with locations (Figs. 1 and 2). As has already been reported by Takahashi and Yasuda (1958), the earliness under short photoperiodic condition at high temperature after vernalization is the most important inner factor which has an intimate bearing on the time of heading, when barleys are sown outdoors in fall at southern locations. Accordingly, it will be expected that different lines with different heading times in the open field differ in their photoperiodic responses. From a simple comparison of heading time under short-day among the different selection lines, therefore, it is difficult to know exactly the differences in the effects of natural selection on their sensitivities to short-day. For the reason stated above, the location-effects upon sensitivity to short-day were investigated using the lines which were similar in heading time when sown outdoors in fall at Kurashiki. For comparisons in the early selection groups, the lines with heading time of April 12~24 and those of April 23~28 at Kurashiki have been used in Crosses No. 1 and No. 3, respectively, with the hope that the heading times of the most selection lines of each of the four locations are included in these ranges.

As seen in Table 6, the group means are always largest in the selections from Morioka, and tend to become smaller as growing locations go down to

TABLE 6

Mean days to flag-leaf emergence under short-day after vernalization and their differences among locations in early selection lines which were similar in heading time when simultaneously sown outdoors in fall at Kurashiki

(A) Cross No. 1 (Heading time in open field : April 12~24)

Item	$\bar{x} \pm s_{\bar{x}}$	Morioka $\bar{x} \pm s_{\bar{x}}$ 63.95±0.6868	Konosu $\bar{x} \pm s_{\bar{x}}$ 63.78±1.5625	Kurashiki $\bar{x} \pm s_{\bar{x}}$ 61.43±1.6434
Kanoya	61.36±0.2918	2.59**	2.42**	0.07
Kurashiki	61.43±1.6434	2.52**	2.35**	
Konosu	63.78±1.5625	0.17		

** Significant at 1% level.

(B) Cross No. 3 (Heading time in open field : April 23~28)

Item		Morioka	Konosu	Kurashiki
		$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$
	$\bar{x} \pm s_{\bar{x}}$	82.39±0.8249	78.75±0.9958	78.44±0.8044
Kanoya	76.88±0.5195	5.51**	1.87**	1.56**
Kurashiki	78.44±0.8044	3.95**	0.31	
Konosu	78.75±0.9958	3.64**		

** Significant at 1% level.

south. The difference in group mean between Morioka and Kanoya selections is about 3 days in Cross No. 1 and about 6 days in Cross No. 3. These differences are significant at the 1 percent level of probability. Difference in group mean between Konosu and Kurashiki selections is also remarkable and statistically significant in Cross No. 1, but is only slight in Cross No. 3.

In mid-season groups, comparison of group means was made by the use of the lines which headed during from April 29 to May 5 in Cross No. 1, and those which headed during from April 28 to May 1 in Cross No. 3 (Table 7).

TABLE 7

Mean days to flag-leaf emergence under short-day after vernalization and their differences among locations in mid-season selection lines which were similar in heading time when simultaneously sown outdoors in fall at Kurashiki

(A) Cross No. 1 (Heading time in open field : April 29~May 5)

Item		Morioka	Konosu	Kurashiki
		$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$
	$\bar{x} \pm s_{\bar{x}}$	65.21±0.8775	64.03±0.2531	64.78±0.5309
Kanoya	63.67±0.7776	1.54**	0.36	1.11**
Kurashiki	64.78±0.5309	0.43	−0.75	
Konosu	64.03±0.2531	1.18		

** Exceeds the 1% level.

(B) Cross No. 3 (Heading time in open field : April 28~May 1)

Item		Morioka	Konosu	Kurashiki
		$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$
	$\bar{x} \pm s_{\bar{x}}$	82.80±0.8789	79.61±0.8887	81.80±1.6658
Kanoya	78.87±1.9508	3.93**	0.74	2.93*
Kurashiki	81.80±1.6658	1.00	−2.19*	
Konosu	79.61±0.8887	3.19**		

* and ** exceed the 5% and 1% levels, respectively.

It is obvious in Table 7 that group mean is, as in the early selection group, the largest in Morioka and the smallest in Kanoya. The differences in group means between them are 2 days or more, and exceed the 1 percent level of probability. It is also observed in the same table that the selection groups from Konosu always show slightly early in average as compared with those from Kurashiki.

In late selection groups, it was impossible to take even 5 lines which indicated a similar heading time under outdoor condition at Kurashiki, because differences in heading time under outdoor condition among lines from different locations had been too large in this late selections as compared with the other selection groups (Figs. 1 and 2). For the reason, comparisons in mean days to flag-leaf emergence among groups were made between every two locations, which were shown in Tables 8A and 8B.

As seen in Tables 8A and 8B, the group means of Morioka selections

TABLE 8

Mean days to flag-leaf emergence under short-day after vernalization and their differences between locations in late selection lines which were similar in heading time when simultaneously sown outdoors in fall at Kurashiki

(A) Cross No. 1 (Heading time in open field : May 13～17)

Morioka $\bar{x} \pm s_{\bar{x}}$	Kurashiki $\bar{x} \pm s_{\bar{x}}$	Difference
75.98±0.9327	74.61±1.2205	1.31*

* Exceeds the 5% level.

(B) Cross No. 3

Heading time in open field : May 1～3	$\bar{x} \pm s_{\bar{x}}$	Heading time in open field : May 4～7	$\bar{x} \pm s_{\bar{x}}$
Konosu	88.30±1.4280	Morioka	88.70±1.5600
Kanoya	87.46±1.6989	Kurashiki	86.31±1.0611
Difference	0.84	Difference	2.39**

** Exceeds the 1% level.

always 1～2 days larger in both crosses than those of Kurashiki selections, and these differences are significant at 5 percent or 1 percent levels of probability. On the other hand, a comparison between Konosu and Kanoya is made only for Cross No. 3, and it is found from Table 8B that the selections from Konosu are slightly later than those from Kanoya, though the difference between them is statistically insignificant.

From these results, there seems no doubt that in any of the three groups, the lines from northern locations like Morioka tend to be later in heading than those from southern locations when grown under short-day at high temperature after vernalization. In other words, it may be said that the lines from northern locations are more sensitive to short-photoperiod as compared with those from southern locations.

4. *Response of Vernalized Plants to Long-day (Earliness in a Narrow Sense)*

Responses of vernalized plants to long-photoperiod at high temperature were investigated only about the selection groups derived from the populations of Morioka and Kurashiki in Cross No. 1. Both Morioka and Kurashiki were hereupon taken as a representative of growing locations under studies. Since there were little differences in long-day response among populations in Cross No. 3 (Yasuda, 1961), selection groups in this cross were not used for the comparison. In Table 9 are shown mean days to flag-leaf emergence and its standard errors in each of the early, mid-season and late selection groups.

TABLE 9

Group mean and its difference between locations of days to flag-leaf emergence under long-day after vernalization in selection lines of Cross No. 1 derived from Morioka and Kurashiki populations

Selection group	Morioka $\bar{x} \pm s_{\bar{x}}$	Kurashiki $\bar{x} \pm s_{\bar{x}}$	Difference
Early	29.24±0.2277	30.09±0.3370	−0.85*
Mid-season	29.06±0.3478	30.38±0.4465	−1.32*
Late	32.71±0.5442	30.71±0.5264	+2.00**

Parent : Iwate Omugi No. 1 34.32±0.4403 ; Indian Barley 28.71±0.0192

* and ** exceed the 5% and 1% significant levels, respectively.

As seen in Table 9, there are little differences in mean days among groups of Kurashiki. Among the groups of Morioka, on the other hand, the late group is about 4 days later than those of the early and mid-season groups, though no appreciable differences are found between the early and mid-season groups. A comparison between locations shows that the selections from Morioka are one day earlier in average time of flag-leaf emergence in both the early and mid-season groups than those from Kurashiki. The result of the late group is quite the reverse of those of the early and mid-season groups. Variances within group are generally larger in the selection groups of Morioka than those of Kurashiki.

Furthermore, the effects of natural selection on this inner factor were also compared, as well as in analysis of sensitivity to short-day, by the use of the lines which were almost similar in heading time when sown outdoors in fall at Kurashiki (Table 10). As shown in Table 10, the results are quite the same as those in Table 9 obtained from all selection lines. It may therefore be safely concluded from these results that the early and mid-season type plants selected from the populations grown at high latitudinal locations are earlier in heading under continuous illumination at high temperature after vernalization as compared with those from the populations grown at low latitudinal locations. However, effect of natural selection on this factor seems not to be so strong as on the sensitivity to short-day.

TABLE 10

Group mean and its difference between locations of days to flag-leaf emergence under long-day after vernalization in selection lines which were similar in heading time when simultaneously sown outdoors in fall at Kurashiki

Selection group	Heading time at Kurashiki (Fall-sown)	Morioka $\bar{x} \pm s_{\bar{x}}$	Kurashiki $\bar{x} \pm s_{\bar{x}}$	Difference
Early	(April 12~24)	29.25±0.2298	30.28±0.3631	−1.03**
Mid-season	(April 29~May 5)	29.33±0.3825	30.58±0.4904	−1.25**
Late	(May 13~17)	32.65±0.9266	31.61±0.6099	+1.04*

* and ** exceed the 5% and 1% significant levels, respectively.

IV. DISCUSSION

From the results of this experiment, the characteristics of the selections from the populations grown at different locations will be shown as below.

<table>
<tr><th>Location</th><th>Heading time (when sown outdoors at Kurashiki)</th><th>Spring and winter habit of growth</th><th>Sensitivity to photoperiod after vernalization</th></tr>
<tr><td>Morioka</td><td>many very late and extremely late types, but a few very early type depending upon crosses</td><td>winter type</td><td>head later under short-day condition (long-day type), but earlier under long-day condition</td></tr>
<tr><td>Konosu</td><td>without extremely early type, but a few extremely late type depending upon crosses</td><td>both spring and winter types</td><td rowspan="3">head earlier under short-day condition (day-neutral type)</td></tr>
<tr><td>Kurashiki</td><td>both extremely early and extremely late types</td><td>both spring and winter types</td></tr>
<tr><td>Kanoya</td><td>without both extremely early and very late types</td><td>spring type</td></tr>
</table>

These results seem to be almost the same as those obtained from the analysis of the populations (Yasuda, 1961), but are still different in some points. First, it must be mentioned that extremely early type lines were not found in Kanoya selections, in spite of the fact that Kanoya was located in southernmost regions and had the mildest winters among four locations. This differed slightly from the results of the population analysis suggesting a general tendency that the average heading times of the populations became earlier as the growing locations went down to south. Kanoya selections, however, entirely lacked very late type lines, and almost all of them consisted of the lines which headed comparatively earlier than those of the other locations. It may be considered, therefore, that such results of the selections well explain the tendency as shown in the populations. In any way, it may be safely said that very early and late type plants are not so adaptive to such a lower latitudinal place like Kanoya.

In the present experiment, furthermore, the extremely early and late type lines were found in the early and late selection groups, respectively, derived from Kurashiki populations. Accordingly, the variability within selections is generally larger in the selections from Kurashiki than in those from the other locations, so far as heading times in the open field are concerned. This suggests that the pressure of natural selection for barley plants is considerably relaxed, allowing survival of various types of barley, when barley hybrid populations have been grown successively at Kurashiki, and, therefore, that the environmental conditions in Kurashiki is favorable to the growth of various types of barley. Though the climatic condition in Konosu seems not so much different from in Kurashiki, extremely late type lines could hardly be found among Konosu selections, and consequently, the variation within the selection was relatively small.

As to spring and winter habit of growth, a good agreement was obtained between the results with the selections and those with the populations; both results indicated that the most remarkable difference was found between Morioka and the other locations. This suggests that winter type have selective advantage over spring type at the high latitudinal place like Morioka, but Konosu or Kurashiki where latitude is comparatively lower, are generally favorable for the growth of both spring and winter types. However, winter type seems to be no longer adaptive to the further low latitudinal region, represented by Kanoya.

It seems, however, that adaptability of spring type plants vary slightly with their genotypic constitutions regarding spring and winter habit of growth. Among five kinds of genotypes for spring habit involved in Cross No. 3, the frequency of the lines with $ShShSh_2^{II}Sh_2^{II}$ genotype is always by far higher than those of the theoretical ones in Konosu and its southern locations, and this tendency is especially marked in the early selection group. On the other hand, the frequencies of the lines with the other spring genotypes are almost the same as the expected. Therefore, predominance of spring type lines in the selections from the locations south to Konosu included is, perhaps, caused by the spring type lines with $ShShSh_2^{II}Sh_2^{II}$ genotype. This has previously been verified by the population analysis. And, the finding of Takahashi and Yasuda (1956) that almost all of spring barley varieties native to Japan belong to this genotype may support the above-mentioned conclusion.

It is well-known that day-length is one of the most important external factors determining adaptabilities of crops. Doroshenko (1927), Forster *et al.* (1932), Forster and Vasey (1935) and Allard (1941) have reported that local varieties of same crops differed in sensitivity to photoperiod with their origins. According to Takahashi and Yasuda (1958), responses of vernalized barley plant to short-day have an intimate bearing on the earliness of fall-sown barleys, and correlation coefficients between them always show significant positive high values regardless of variety or hybrid. These facts led us to investigate the differences in response to short-day among selections using the lines which were similar in heading time when simultaneously sown outdoors in fall at Kurashiki, and it was found that mean days to flag-leaf emergence under short-day condition were always the largest in the selection group from Morioka, and tended to become smaller as the locations went down to south. This is easily expected from the analysis of the populations. Nevertheless, the results obtained from the selections have very important implications differing from those of the populations, because the former shows that the effects of natural selection have been exerted upon short photoperiodic sensitivity itself, regardless of heading times in the open field. In any way, these results may suggest that long-day type (sensitive to short-day) and day-neutral type (insensitive to short-day) are adaptive to high and low latitudinal regions, respectively.

About the response to long-day after vernalization, the situation was more or less different from the expectation based on the analysis of the populations. The previous finding that the average time of flag-leaf emergence under long-day condition after vernalization was latest in Morioka populations and became earlier as the growing locations went down to south, was confirmed only by the late selection lines in the present experiment. In the early and mid-season selection lines, on the contrary, time of flag-leaf emergence under such condition was early in Morioka selections and late in Kurashiki selections. Retardation of time of flag-leaf emergence under long-day condition in Morioka populations however, seems to be explained by the fact that Morioka populations have chiefly consisted of such very late or extremely late type plants as found in the late selection group from Morioka in the present experiment with respect to heading time in open field. However, it has already been known that this inner factor was not so affected directly the earliness of barleys sown outdoors in fall at southern location as compared with short-day response (Takahashi and Yasuda, 1958, 1960). Nevertheless, it is conceivable from the result in the present study that the sensitivity to long-day after vernalization may play a significant role in determining heading time in open field of barley plants which are grown at northern location like Morioka wherein longer day length predominates during heading time.

Among the external factors, both light (day-length) and temperature are very important in considering the effect of environment. They operate together on plants, and the differences in the effects of natural selection on such inner factors as growth habit and photoperiodic responses cannot be attributed only to the different in either day-length or temperature among locations. The environment should be rather regarded as an interaction between the individual external factors such as day-length, temperature and others. Nevertheless, it may be said that the relative importance of day-length or temperature in the effect of environment on the inner factors varies with the relation between times of manifestation of these inner factors and seasonal changes of climate. As to spring and winter habit of growth, the differences in effect of natural selection on the populations may chiefly be attributable to the differences in temperature conditions during from winter to early spring. Thereafter, as a consequence of rise of temperature, natural selection seems to exert an influence upon their responsibilities of vernalized plants to photoperiods.

Finally, from the viewpoint of the breeding practice, barley plants with the following nature seem to be adaptive to respective regions, so far as heading time is concerened: In northern region, represented by Morioka in this experiment, barley plants are necessary to have at least a nature of relatively late heading with winter habit. If earlier varieties are needed, the winter habit should be combined with a nature of earlier heading under long-day after vernalization. On the other hand, early to medium-early type plants of both spring and winter habit are more adaptive to central and southern regions, represented by Konosu and Kurashiki. Southernmost region like Kanoya is favorable for early and medium early plants combined with spring habit, but not for extremely early and late and also winter type plants. In the regions south to Konosu included, however, it must be mentioned that among spring type plants, the plants with $ShShSh_2^{II}Sh_2^{II}$ genotype are more adaptive to these regions as compared with other genotypes. For breeding of earlier varieties adaptive to these regions, day-neutral type plants seem to be useful. The earliness in a narrow sense (sensitivity to long-day after vernalization) is not so important for this purpose, however.

The materials used in this experiment consisted of the plants derived from the populations which were grown successively during several generations. They must have been subjected to the effects of competition among different genotypes. Therefore, local adaptabilities indicated in the present study may somewhat differ from those in pure stand. In the present study, moreover, a productivity was not considered. These problems will be dealt with in other publications.

V. SUMMARY

Two crosses of barley were successively grown in bulk from F_2 up to F_5 generations at four locations; Morioka (North), Konosu (Central), Kurashiki (South) and Kanoya (Southernmost). The early, mid-season and late type plants were selected at respective locations from F_6 generation of these hybrid populations. These selections were investigated about their genotypic constitutions for heading time in open field and its inner factors, spring and winter habit of growth, photoperiodic response (response of vernalized plants to short-day) and "earliness in a narrow sense" (response of vernalized plants to long-day). The results obtained are summarized as follows:

1) When sown simultaneously outdoors in fall at Kurashiki, the early, mid-season and late groups of selections from each of the four locations headed also in this order. The extremely early type plants could be found among the early selection groups from Konosu and Kurashiki, but not among those from Morioka and Kanoya. On the other hand, extremely late type lines were found among the late selection groups from Morioka and Kurashiki, but not among those from Kanoya. Thus, Kurashiki selections were the most variable as to the heading time under outdoor condition.

2) Regardless of selection groups, winter type predominated in Morioka selections (70% or more), while in the selections from the places south to Konosu included, about 60 percent or more lines were spring type. There were only a little winter type lines among Kanoya selections, but Kurashiki selections involved more winter types than Konosu selections.

3) In the spring type lines from Cross No. 3 including two kinds of spring genes, *sh* and Sh_2^{II}, frequency of $ShShSh_2^{II}Sh_2^{II}$ genotype was higher than the other genotypes in the selections from the places south to Konosu included. This type seems to be most adaptive to the regions of southern Japan.

4) Mean days to flag-leaf emergence under short-day at high temperature after vernalization were, among the three selection groups, smallest in the early group and largest in the late group, regardless of locations. Differences in the sensitivity to short-photoperiod between selections from different locations were investigated by the use of the lines headed under outdoor condition during the same period, which indicated that mean days to flag-leaf emergence were always the largest in the selection group from Morioka and tended to become smaller as the locations went down to south.

5) Morioka and Kurashiki selections of Cross No. 1 were studied as to difference in time of flag-leaf emergence under long-day at high temperature after vernalization. In the early and mid-season groups, time of flag-leaf emergence was always earlier in Morioka selections than in Kurashiki ones.

6) These results suggest that barleys having a nature of relatively late heading or sensitive to short-day combined with winter habit are adaptive to northern regions. On the other hand, central and southern regions are, in general, favorable to the growth various type of barleys, though extremely early and extremely late types are less adaptive to central region than to southern one. Southernmost region are favorable to early to medium-early barleys with spring habit, but not to extremely early and late and also winter type ones.

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